

## Dawn singing in Brown Creeper (*Certhia americana*)

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Marini, K.L.D., S. Nadon, and J.R. Foote. 2020. Dawn singing in Brown Creeper (*Certhia americana*). Canadian Field-Naturalist 134(2): 117–124. <https://doi.org/10.22621/cfn.v134i2.2139>

### Abstract

The dawn chorus of birds is an impressive display in which many individuals of a variety of species sing concurrently before sunrise. Brown Creeper (*Certhia americana*) is a small passerine bird that has not been well studied and is thought not to sing during the dawn chorus. Here, we used automated recordings to analyze Brown Creeper singing during the 2015–2017 breeding seasons from April through August in order to identify patterns in the timing and quantity of singing. We found that Brown Creepers did sing before sunrise, most often between April and early June and then more sporadically through mid July. We did not find any seasonal changes in song rates before sunrise, but we did find non-linear seasonal trends in both the timing and total duration of dawn singing bouts. Dawn choruses began earlier and lasted longer from April through mid June after which they began later and became shorter. Our results highlight the benefit of using automated recording techniques to study natural history of difficult to study species and add to our understanding of Brown Creeper natural history.

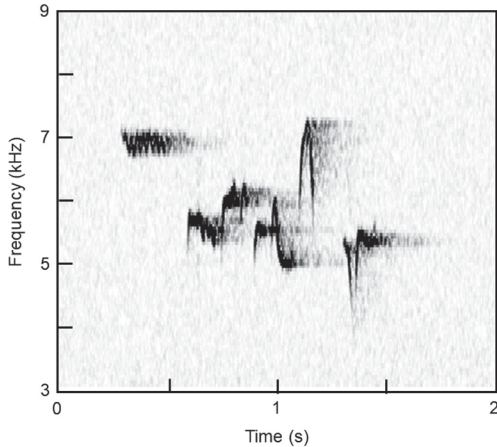
Key words: Dawn chorus; vocal behaviour; Brown Creeper; autonomous recording

### Introduction

During the breeding season, territorial males of many bird species participate in daily bouts of extended singing prior to sunrise, in a communication network commonly known as the dawn chorus (Staicer *et al.* 1996; Gil and Gahr 2002; Burt and Vehrencamp 2005). Several hypotheses exist as to why birds sing before sunrise (see Staicer *et al.* 1996), including environmental influences (e.g., low light levels could make for poor foraging; Kacelnik 1979), intrinsic factors (e.g., circadian rhythms or hormones; reviewed in Staicer *et al.* 1996; Greives *et al.* 2015), or social explanations (e.g., territory defence; Amrhein and Erne 2006; or maintaining relationships with neighbours; Foote *et al.* 2008). Song output during the dawn chorus is also often an honest signal of male quality (Gil and Gahr 2002), allowing females to compare the quality of their mate against his neighbours and make decisions about extra-pair copulations (e.g., Otter *et al.* 1997; Suter *et al.* 2009). The characteristics of the dawn chorus (e.g., start time, duration, and song rate) often show seasonal variation and may show distinct patterns. Different characteristics of the dawn chorus may: 1) peak early in the season and gradually decline (e.g., Mace 1987), 2) remain relatively constant across the breeding season (e.g., Kunc *et al.* 2005), 3) build toward a mid-

season peak and then decline (e.g., Davis 1958), or 4) peak in particular breeding stages (e.g., Bruni and Foote 2014).

Not all species sing extensively before sunrise, and, for some species, we lack knowledge about their singing habits and behaviours. Brown Creeper (*Certhia americana*) is one such species. A small, cryptically-coloured passerine in the Certhiidae family, Brown Creeper is the only North American species of treecreeper (Poulin *et al.* 2020). Brown Creepers are old forest specialists, and are common across much of North America, preferring to nest in habitats with high densities of large-diameter trees and snags (Poulin *et al.* 2008). While the syllables and song structure of Brown Creeper are fairly well described (e.g., Baptista and Johnson 1982; Baptista and Krebs 2000), there is little previous research on its singing behaviour. Brown Creeper sing a single short song (~ 1.2 s) composed of 4–9 high-frequency notes that is thought to be sung only by males (Poulin *et al.* 2020; Figure 1). Brown Creepers have not been identified singing before sunrise during the dawn chorus. However, there has not been a study of the phenology or daily pattern of singing (Poulin *et al.* 2020) and two congeneric European treecreeper species sing before sunrise (Santema *et al.* 2019). Much of what we do know about the singing behaviour comes from the



**FIGURE 1.** Spectrogram of Brown Creeper (*Certhia americana*) song.

1978 nesting study by Davis, in which Brown Creeper nests were monitored and some general observations of vocal behaviour were made. Davis (1978) reports anecdotally that Brown Creepers sang territorially and engaged in counter-singing with neighbours, most often beginning in April through to early June. Singing rates were described as increasing during territory establishment and with increased levels of intraspecific competition. Davis (1978) describes male Brown Creepers as singing one to eight songs per minute, with singing bouts lasting 1–22 minutes. These singing bouts occurred ‘sporadically’ through the day, with singing documented as early as 0450 and as late as 1917, although there is no specific mention of singing before sunrise. Singing was also documented during nest building; while females collected nesting material, males were noted singing close by (Davis 1978).

Here, we analyzed recordings made with automated recording units to examine the singing behaviour of Brown Creepers (*C. americana americana*) during the breeding season to determine if Brown Creepers sing before sunrise, and if so, to describe and quantify any seasonal changes in timing or patterns of singing behaviour. Automated recording is advantageous when species are either sensitive to intrusions, such as those caused by human observers, or are difficult to locate and observe (Blumstein *et al.* 2011). Previous research did not identify Brown Creepers as being particularly sensitive to human disturbance (Gutzwiller *et al.* 1994); however, they are cryptic and have a soft high-frequency “tinkling” song (Tyler 1948) that may be difficult to hear, thus automated recordings could be an effective technique for recording Brown Creeper singing.

## Methods

### *Study species and site description*

We recorded in Hiawatha Highlands Conservation Area, Sault Ste. Marie, Ontario, Canada (46.588°N, 84.292°W) from late March/early April through the end of August, 2015–2017 (see Table S1 for dates by recorder) as part of a project for long-term monitoring of bird community composition and vocal behaviour. This conservation area is comprised primarily of mature Sugar Maple (*Acer saccharum* Marshall), Eastern White Pine (*Pinus strobus* L.), and Balsam Fir (*Abies balsamea* (L.) Miller; Sault Ste. Marie Region Conservation Authority 2015; see Foote *et al.* 2018 for further habitat description). While some populations migrate, many populations of Brown Creeper, including our study population, are year round residents (Poulin *et al.* 2020).

We deployed four song meters in each year (model SM2+ in 2015; Model SM3 in 2016 and 2017; Wildlife Acoustics, Maynard, Massachusetts, USA) for a total of 12 different locations over three years. Recorders were spaced such that they were likely to pick up different birds. Within a year, the nearest-recorder distance averaged  $425 \pm 28.4$  m ( $\pm$  SE) while among years, the nearest recorder distance averaged  $211 \pm 14.9$  m. Nest locations of adjacent pairs ranged from 100 to 200 m and territory size averaged 2.3 to 6.4 ha (Davis 1978) such that locations were independent and were likely several territories apart.

Recorders were programmed to begin recording at astronomical twilight (when the sun is 18° below the horizon), before any species at our site begins their dawn singing bout and only nocturnal singing species are vocally active (Leopold and Eynon 1961; Perrault *et al.* 2014), and continued recording until on average  $74.3 \pm 2.02$  min after sunrise (see mean post-sunrise recording time by recorder in Table S1). Recorders recorded for 59 min followed by a 1 min pause to write files. Recordings were made as wav files at 22 050 Hz (SM2) or 24 000 Hz (SM3) and 16-bit accuracy. The batteries and memory cards in recorders were changed weekly.

### *Recording analysis*

We scanned each recording using Syrinx software (John Burt, Seattle, Washington, USA), and visualized spectrograms with a transformation size of 512 FFT, frequency range of 1000–10 000 Hz, a setting of 10 ms per line, and spectral gain of +5. Recordings from each day at each location were combined using a series list text file that included a 1 min blank sound file between each 59 min recording to account for the pause for file writing and to keep the analysis in real-time. Scanning each recording from beginning to end, we used the time and frequency cursors to annotate

all visible Brown Creeper songs (Figure 1), as well as the sunrise time each morning. Sunrise times were obtained from the National Research Council Canada website (National Research Council Canada 2017). In the event that we detected two Brown Creepers singing simultaneously, we annotated the songs of the loudest male. We added an annotation for the second bird as ‘bird2’ to keep track of instances of potential counter-singing. Eleven of the 12 recorders had singing Brown Creepers and we assume that a bird at a given site is the same individual. Winter (2020) selected 10 songs from our annotations from seven of these locations and found higher spectrogram cross-correlation scores for within location than among locations supporting that the primary singer at each site was a single individual. Once each file was annotated, we calculated the time of the first song relative to sunrise (min), the total duration of singing before sunrise (dawn bout; time of last – first song before sunrise [min]), song rate before sunrise (number of songs before sunrise/duration of dawn chorus [songs/min]), and song rate after sunrise (number of songs after sunrise/recording length post-sunrise [songs/min]) for each location. Our recording equipment failed on 214 nights across the 11 recorders (see Table S1 for details by recorder). We excluded 41 recordings from analysis (17 due to inclement weather making it impossible to transcribe recordings, and 24 due to premature battery failure causing the recordings to end before sunrise), leaving us with 1335 recordings from 11 locations for analysis.

#### Statistical analysis

We constructed generalized additive mixed-effects models (GAMMs) to look at the probability of detection of Brown Creepers on the recordings and at the presence/absence of singing before sunrise (dawn bouts). These models included year and recording date (expressed as day of year, where January 1 = 1; 2016 was a leap year hence the requirement to use Julian dates) as covariates, with recorder location as a random effect, with binomial distributions and logit link function. We also constructed GAMMs for singing start time relative to sunrise, total duration of dawn bout (minutes), pre-dawn song rate (songs/min). These models also included year, recording date, and male ID as a random effect. An additional model for song rate included period of the day (before or after sunrise) to compare song rates between these two periods.

Best models were selected by backwards stepwise regression based on AIC, and in instances where the estimated degrees of freedom (edf) for the smooth terms were close to 1 (indicating a potential linear relationship), we refit the models as generalized linear mixed-effects models (GLMM). We followed Zuur *et al.* (2014) to build and validate GAMMs, and our

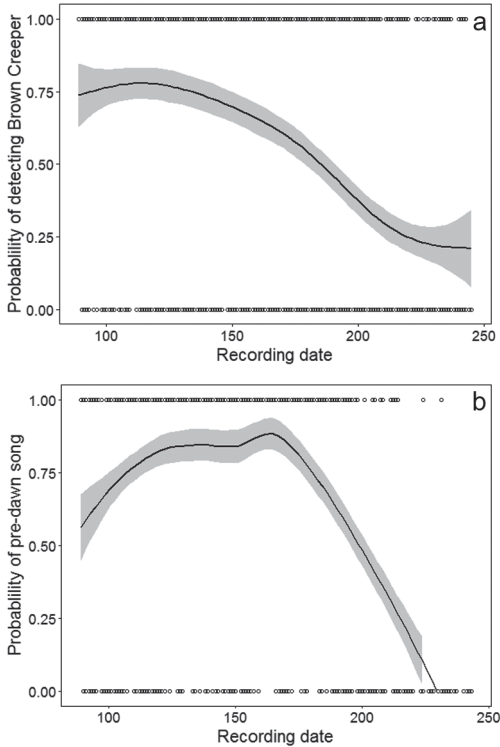
smooth terms were constructed using thin plate regression with shrinkage. We identified three males that could be problematic in the analysis (one due to much greater song output and two due to fewer days with singing compared to other locations), however when we re-ran the analyses without these data, most of the resulting top models and significance of terms did not differ. We present the results from models including all data, and in instances where the removal of any/all of these males changed the best model, we present results both with and without these males.

All analyses were done in R (v.3.4.2; R Core Team 2017) using the ‘mgcv’ package (v.1.8-23; Wood 2018) for GAMMs, with ‘lme4’ package (v.1.1-15; Bates *et al.* 2015) for GLMMs, and graphics made with ‘ggplot2’ package (v.2.2.1; Wickham 2016). We used the ‘lmerTest’ package (v.2.0-36; Kuznetsova *et al.* 2017) to calculate *P*-values for GLMMs via Satterthwaite’s degrees of freedom method. The *P*-values obtained for GAMM models are estimates, and as such, values that are marginally significant should be interpreted with caution (Zuur *et al.* 2009). For all results, we report means  $\pm$  SE.

## Results

We identified Brown Creeper songs on 54.4% (726/1335) of recordings, and of these, 64.2% (466/726) of recordings included Brown Creepers singing one or more songs before sunrise (Figure 2). Date had a non-linear relationship with both the probability of detecting a Brown Creeper (smooth term:  $r^2 = 0.163$ ,  $F_{3,11} = 26.87$ ,  $P < 0.0001$ ; Table S2, Figure 2a) and the probability of pre-dawn song (smoother term:  $r^2 = 0.294$ ,  $F_{5,42} = 14.09$ ,  $P < 0.0001$ ; Table S2, Figure 2b).

The average start time of the first singing bout of the morning was  $5.61 \pm 1.10$  min before sunrise (range: 80.6 min before dawn to 129.2 min after dawn,  $n = 726$ ). For mornings with a dawn bout (song beginning before sunrise), the start time of singing averaged  $21.75 \pm 0.47$  min before sunrise (range: 0.50–80.60 min before sunrise,  $n = 466$ ). The start time of dawn bouts relative to sunrise changed through the season, with a strong non-linear relationship with date (smoother term:  $r^2 = 0.17$ ,  $F_{4,70} = 5.17$ ,  $P < 0.0001$ ; Table S3, Figure 3). Brown Creepers started singing well before sunrise in the early to mid-breeding season (April–mid June; Julian dates 89–160). By mid June (~Julian day 170), Brown Creepers began to sing closer to sunrise and eventually stopped singing a dawn bout (Figure 3). The latest dawn chorus was recorded on 12 August (Julian 224), however, the mean last chorus date among 11 recorders was 18–19 July (Julian 200). Four males stopped singing a dawn bout for 17–39 days before resuming dawn song for

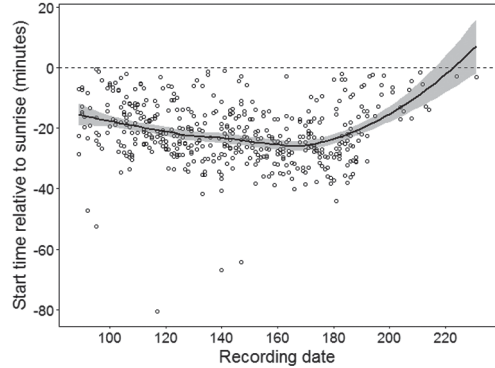


**FIGURE 2.** Probability of detecting Brown Creeper (*Certhia americana*) song a. at any time of day and b. before dawn by recording date. Open circles are the observed data, and black lines show the relationship between recording date (Julian day) and response variables obtained from GAMMs, with the grey areas representing the 95% CI for the smooth functions.

several days. The mean date of initial chorus cessation excluding these several late choruses was 8–9 July (Julian 180).

The average duration of a Brown Creeper dawn chorus was  $13.29 \pm 0.45$  min (range: 0.25–51.33 min). Our best model for duration of singing included significant terms for recording date and year (smoother term for date:  $r^2 = 0.17$ ,  $F_{3,96} = 5.17$ ,  $P < 0.0001$ ; Table S3). Similar to the pattern we found with start time, the total duration of singing appeared to change around mid June. During the early to mid-breeding season (April through mid June; Julian 89–160) there was a trend of increasing duration, peaking around mid June (~Julian 170), after which the total duration of Brown Creeper dawn singing activity decreased steadily (Figure 4).

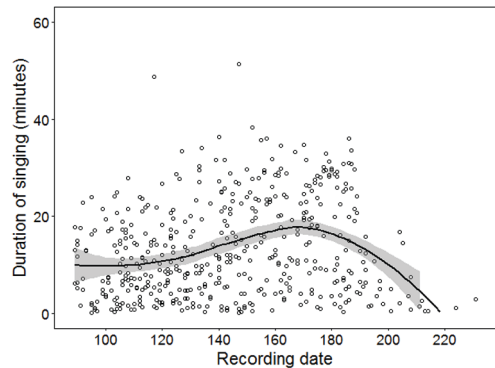
As we found no evidence of non-linear relationships between recording date and song rate, we constructed GLMMs to examine dawn chorus song rates. Song rate during the dawn chorus was not signifi-



**FIGURE 3.** Start time of the dawn chorus of Brown Creeper (*Certhia americana*) relative to sunrise (dashed line indicates sunrise). Open circles are observed data, while the black line represents the non-linear relationship between start time and recording date (Julian day), based on the output of the GAMM; grey regions indicate the 95% CI.

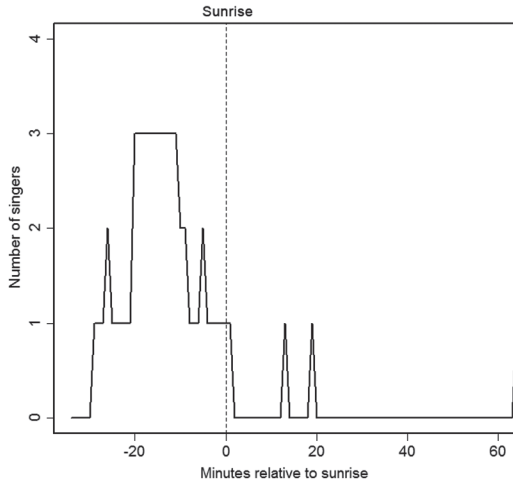
cantly related to date (Table S4). We detected Brown Creeper less often after sunrise ( $n = 343$  recordings) compared to before sunrise ( $n = 466$  recordings). Brown Creeper sang at a significantly higher rate before ( $3.9 \pm 0.15$  songs/min) compared to after sunrise ( $3.6 \pm 0.09$  songs/min; Table S4).

To determine if the dawn bouts of different Brown Creeper overlapped, we plotted the number of males singing from the beginning to the end of recording for a randomly chosen date (5 May 2017), from among dates when all recorders were working properly (Table S1) and in the period where most birds sing a dawn bout (Figure 2). Before sunrise, 2–3 birds often sang concurrently while after sunrise only one



**FIGURE 4.** The relationship between the duration of pre-dawn singing of Brown Creeper (*Certhia americana*) and recording date (Julian day). Open circles are observed data, while the black line represents the non-linear relationship between duration of the dawn chorus and recording date, based on the output of the GAMM; grey regions indicate the 95% CI.

bird was recorded singing at any given point in time (Figure 5). Additionally, we examined our annotation files to determine when we recorded a second distant Brown Creeper before sunrise. On average  $2.4 \pm 0.99\%$  of recordings included two singing Brown Creeper before sunrise (range: 0–4.2%).



**FIGURE 5.** Number of Brown Creeper (*Certhia americana*;  $n = 4$ ) singing in each minute of recording from the beginning of singing before sunrise to the end of the recording on 5 May 2017.

## Discussion

We show that Brown Creepers sing a pronounced bout before sunrise during the dawn chorus and sing at a rate that exceeds daytime singing. We show that the probability of detecting Brown Creeper singing before sunrise, and both start time and duration of the dawn bout are related to date with a pronounced drop in activity in mid June with birds mostly stopping singing before sunrise by mid July. Our results are similar to Davis' (1978) general description of daytime vocal behaviour from a similar latitude (~140 km south of our site). During the breeding season, song rate remains constant during the dawn bout. Brown Creepers are fairly cryptic and understudied and we provide the first seasonal study of dawn vocal activity in this species.

The average start time of Brown Creeper dawn bouts was nearly 22 min before sunrise and thus begins in the middle to later period of the dawn chorus (Allard 1930; Leopold and Eynon 1961; Staicer *et al.* 1996). Between approximately April 10 (Julian day = 100) and the first week of July (Julian day  $\approx$  190), males began singing before dawn on most days (Figure 2a). The seasonal pattern of variation in start time of the dawn bout is similar to that observed in other species (e.g., Bruni *et al.* 2014; Zhang *et al.*

2015) including Spotted Towhee (*Pipilo maculatus*), a species that sings earlier relative to sunrise in the peak of the breeding season, which corresponds with males reaching maximum gonadal development (30–60 min; Davis 1958). Other species show a more linear decline in dawn bout start time (e.g., Bruni *et al.* 2014) or show no relationship between start time and date (e.g., Leopold and Eynon 1961; Pérez-Granados *et al.* 2018).

We also found that singing bouts tended to lengthen in the early breeding season, peaking around mid June, before shortening thereafter. While there are fewer studies of dawn bout length in relation to date, our results for Brown Creeper are similar to other species. In Field Sparrow (*Spizella pusilla*), dawn bout length was related to breeding stage, increasing in the fertile stage and then decreasing afterward (Zhang *et al.* 2015). Although not related to date directly, the pattern is similar to our seasonal pattern of longer bouts mid-season. In Collared Flycatcher (*Ficedula albicollis*), dawn bout length declines toward the end of the breeding season, once young have hatched and in Cerulean Warbler (*Setophaga cerulea*), bout length decreased with date (MacDonald and Islam 2019). The patterns in pre-dawn singing of Brown Creeper have an inflection point around early–mid June, which are likely tied to the hatching and fledging of young. Davis' (1978) nesting study showed that young hatch typically in early–late June and all young were fledged by mid June to late July, which is when we see a significant change in the likelihood of singing (around hatching) and the end of singing (around fledging).

We did not find a seasonal pattern in average dawn song rates. Other studies have found relatively consistent seasonal song rates while other chorus properties have remained constant (e.g., Olinkiewicz and Osiejuk 2003; Kunc *et al.* 2005). Dawn song rate has been linked to male quality and reproductive success (e.g., Otter *et al.* 1997; Poesel *et al.* 2001) and is repeatable (Murphy *et al.* 2008) but also relates to the intensity of response to intruders later in the day (Poesel *et al.* 2004) and the likelihood of intrusion (Naguib *et al.* 2001). Perhaps we see that song rate remains seasonally consistent because it is an indicator of quality to both mates and rivals in Brown Creeper. However, some studies have shown the song rate does also decline with date (e.g., Pärt 1991; Dolan *et al.* 2007) and so the characteristics that remain consistent or change seasonally may vary among species.

The range of Brown Creeper song rate reported by Davis (1978) was 1–8 songs/min, which is consistent with our observed song rates before dawn (range: 0.13–8.32 songs/min). We found that song rates were significantly higher before sunrise than after sunrise



as has been shown in many other passerines (reviewed in Staicer *et al.* 1996). Davis (1978) observed that singing rates increased with increasing intraspecific territorial competition but did not measure song rates or compare them among contexts. Our recorder density was not conducive to examining counter-singing interactions, however, we did detect two individuals singing in just over 2% of recordings. Future studies with more densely spaced arrays of recorders (e.g., Mennill *et al.* 2012) covering mapped territories could be used to study counter-singing in this species.

Brown Creepers had already begun to sing when our study began. However, an earlier description by Tyler (1948) suggests that they begin to sing just as March ends. Some of the variation in the probability of detecting a Brown Creeper on a recording was likely due to individuals moving as our recorders were at fixed locations. A further limitation of our study is that we did not identify or monitor individuals in the field, and thus lack information such as the pairing status or reproductive stage of individuals in the population. Without these, our understanding of the singing behaviour of Brown Creepers is still incomplete, and further research is needed to explore the relationships between breeding stage and singing behaviour. Additional factors such as age (Poessel *et al.* 2006), food availability (Berg *et al.* 2005), condition (Murphy *et al.* 2008), neighbourhood density (Liu 2004), and social status (Otter *et al.* 1997) may also influence singing behaviour and should also be addressed in future research. Although many knowledge gaps remain, the results of this study help increase our understanding of Brown Creeper dawn singing and identify areas of inquiry for future research.

### Author Contributions

Writing – Original Draft: K.L.D.M., S.N., and J.R.F.; Writing – Review & Editing: J.R.F.; Conceptualization: K.L.D.M., S.N., and J.R.F.; Investigation: K.L.D.M., S.N., and J.R.F.; Methodology: K.L.D.M., S.N., and J.R.F.; Formal Analysis: K.L.D.M. and J.R.F.; Funding Acquisition: J.R.F.

### Acknowledgements

We would like to acknowledge that this research was conducted in the Robinson-Huron Treaty territory and that the land on which we worked is the traditional territory of the Anishnaabeg, specifically the Garden River and Batchewana First Nations, as well as Métis People. We thank Hiawatha Highlands Conservation Authority for the land used for this study. This study was funded by the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, and the Ontario Ministry of Research and Innovation. We thank two anonymous review-

ers, the Associate Editor, and Editor for constructive feedback that improved our manuscript. We thank J. Waas, B. Fera, M. Ehnes, L. Hodgson, K. Pearse, M. Thompson, and B. McMurray for assistance in the field and/or lab.

### Literature Cited

- Allard, H.A.** 1930. The first morning song of some birds of Washington D.C.; its relation to light. *American Naturalist* 64: 436–469. <https://doi.org/10.1086/280329>
- Amrhein, V., and N. Erne.** 2006. Dawn singing reflects past territorial challenges in the winter wren. *Animal Behaviour* 71: 1075–1080. <https://doi.org/10.1016/j.anbehav.2005.07.023>
- Baptista, L.F., and R.B. Johnson.** 1982. Song variation in insular and mainland California Brown Creepers (*Certhia familiaris*). *Journal of Ornithology* 123: 131–144. <https://doi.org/10.1007/BF01645053>
- Baptista, L.F., and R. Krebs.** 2000. Vocalizations and relationships of Brown Creepers *Certhia americana*: a taxonomic mystery. *Ibis* 142: 457–465. <https://doi.org/10.1111/j.1474-919X.2000.tb04442.x>
- Bates, D., M. Maechler, B. Bolker, and S. Walker.** 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Berg, M., N. Beintema, J. Welbergen, and J. Komdeur.** 2005. Singing as a handicap: the effects of food availability and weather on song output in the Australian Reed Warbler *Acrocephalus australis*. *Journal of Avian Biology* 36: 102–109. <https://doi.org/10.1111/j.0908-8857.2005.03285.x>
- Blumstein, D.T., D.J. Mennill, P. Clemens, L. Girod, K. Yaom, G. Patricelli, J.L. Deppe, A.H. Krakauer, C. Clark, K.A. Cortopassi, S.F. Hanser, B. McCowan, A.M. Ali, and A.N.G. Kirscehl.** 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations, and prospectus. *Journal of Applied Ecology* 48: 758–767. <https://doi.org/10.1111/j.1365-2664.2011.01993.x>
- Bruni, A., and J.R. Foote.** 2014. Dawn singing of Eastern Phoebes varies with breeding stage and brood number. *Wilson Journal of Ornithology* 126: 500–507. <https://doi.org/10.1676/13-175.1>
- Bruni, A., D.J. Mennill, and J.R. Foote.** 2014. Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. *Journal of Ornithology* 155: 877–890. <https://doi.org/10.1007/s10336-014-1071-7>
- Burt, J.M., and S.L. Vehrencamp.** 2005. Dawn chorus as an interactive communication network. Pages 320–343 in *Animal Communication Networks*. Edited by P.K. McGregor. Cambridge University Press, Cambridge, United Kingdom. <http://doi.org/10.1017/cbo9780511610363.019>
- Davis, C.M.** 1978. A nesting study of the Brown Creeper. Pages 237–263 in *Living Bird*. Edited by D.A. Lancaster and J.R. Johnson. The Laboratory of Ornithology, Ithaca, New York, USA.
- Davis, J.** 1958. Singing behavior and the gonad cycle of the

- Rufous-sided Towhee. *Condor* 60: 308–336. <https://doi.org/10.2307/1365157>
- Dolan, A., K. Sexton, L. Redmond, and M. Murphy.** 2007. Dawn song of eastern kingbirds: intrapopulation variability and sociobiological correlates. *Behaviour* 144: 1273–1295. <https://doi.org/10.1163/156853907781890922>
- Foote, J.R., L.P. Fitzsimmons, D.J. Mennill, and L.M. Ratcliffe.** 2008. Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behavioral Ecology* 19: 1192–1199. <https://doi.org/10.1093/beheco/arm087>
- Foote, J.R., K.L.D. Marini, and H. Al-Ani.** 2018. Understanding the function of nocturnal song in ovenbirds: males do not countersing at night. *Journal of Avian Biology* 49: jav-012511. <https://doi.org/10.1111/jav.01729>
- Gil, D., and M. Gahr.** 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution* 17: 133–141. [https://doi.org/10.1016/S0169-5347\(02\)02410-2](https://doi.org/10.1016/S0169-5347(02)02410-2)
- Greives, T.J., S.A. Kingma, B. Kranstauber, K. Mortega, M. Wikelski, K. van Oers, A.C. Mateman, G.A. Ferguson, G. Beltrami, and M. Hau.** 2015. Costs of sleeping in: circadian rhythms influence cuckoldry risk in a songbird. *Functional Ecology* 29: 1300–1307. <https://doi.org/10.1111/1365-2435.12440>
- Gutzwiller, K.J., R.T. Wiedenmann, K.L. Clements, and S.H. Anderson.** 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *Auk* 111: 28–37. <https://doi.org/10.2307/4088502>
- Kacelnik, A.** 1979. The foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. *Animal Behaviour* 27: 237–241. [https://doi.org/10.1016/0003-3472\(79\)90143-X](https://doi.org/10.1016/0003-3472(79)90143-X)
- Kunc, H.P., V. Amrhein, and M. Naguib.** 2005. Seasonal variation in dawn song characteristics in the common nightingale. *Animal Behaviour* 70: 1265–1271. <https://doi.org/10.1016/j.anbehav.2005.02.010>
- Kuznetsova, A., P.B. Brockhoff, and R.H.B. Christensen.** 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82: 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Leopold A., and A.E. Eynon.** 1961. Avian daybreak and evening song in relation to time and light intensity. *Condor* 63: 269–293. <https://doi.org/10.2307/1365621>
- Liu, W.C.** 2004. The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour* 68: 39–44. <https://doi.org/10.1016/j.anbehav.2003.06.022>
- MacDonald, G.J., and K. Islam.** 2019. Do social factors explain seasonal variation in dawn song characteristics of paired male Cerulean Warblers (*Setophaga cerulea*)? *Bioacoustics*: online. <https://doi.org/10.1080/09524622.2019.1682671>
- Mace, R.** 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature* 330: 745–746. <https://doi.org/10.1038/330745a0>
- Mennill D.J., M. Battiston, D.R. Wilson, J.R. Foote, and S.M. Doucet.** 2012. Field test of an affordable, portable wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution* 3: 704–712. <https://doi.org/10.1111/j.2041-210X.2012.00209.x>
- Murphy, M.T., K. Sexton, A.C. Dolan, and L.J. Redmond.** 2008. Dawn song of the eastern kingbird: an honest signal of male quality? *Animal Behaviour* 75: 1075–1084. <https://doi.org/10.1016/j.anbehav.2007.08.020>
- Naguib, M., R. Altenkamp, and B. Griessmann.** 2001. Nightingales in space: song and extra-territorial forays of radio tagged song birds. *Journal für Ornithologie* 142: 306–312. <https://doi.org/10.1007/BF01651369>
- National Research Council Canada.** 2017. Sunrise/sunset calculator. Government of Canada. Accessed 25 October 2017. <https://www.nrc-cnrc.gc.ca/eng/services/sunrise>.
- Olinkiewicz, A., and T.S. Osiejuk.** 2003. Effect of time of season and neighbours on singing activity in the Corn Bunting *Miliaria calandra*. *Acta Ornithologica* 38: 117–122. <https://doi.org/10.3161/068.038.0208>
- Osiejuk, T.S., and L. Kuczyński.** 2000. Song functions and territoriality in Eurasian Treecreeper *Certhia familiaris* and Short-toed Treecreeper *Certhia brachydactyla*. *Acta Ornithologica* 35: 109–116.
- Otter, K., B. Chruszcz, and L. Ratcliffe.** 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology* 8: 167–173. <https://doi.org/10.1093/beheco/8.2.167>
- Pärt, T.** 1991. Is dawn singing related to paternity insurance? The case of the collared flycatcher. *Animal Behaviour* 41: 451–456. [https://doi.org/10.1016/s0003-3472\(05\)80847-4](https://doi.org/10.1016/s0003-3472(05)80847-4)
- Pérez-Granados, C., T.S. Osiejuk, and G.M. López-Iborra.** 2018. Dawn chorus interpretation differs when using songs or calls: the Dupont's Lark *Chersophilus duponti* case. *Peer J* 6: e5241. <https://doi.org/10.7717/peerj.5241>
- Perrault, K., L.M. Lobert, M. Ehnés, and J.R. Foote.** 2014. Nocturnal singing in a temperate bird community. *Journal of Ornithology* 155: 1059–1062. <https://doi.org/10.1007/s10336-014-1077-1>
- Poesel, A., T. Dabelsteen, and S.B. Pedersen.** 2004. The dawn song of the Blue Tit *Parus caeruleus* and its role in sexual selection. *Ethology* 107: 521–531. <https://doi.org/10.1046/j.1439-0310.2001.00680.x>
- Poesel, A., K. Foerster, and B. Kempenaers.** 2001. Dawn song of male blue tits as a predictor of competitiveness in midmorning singing interactions. *Acta Ethologica* 6: 65–71. <https://doi.org/10.1007/s10211-004-0086-0>
- Poesel, A., H.P. Kunc, K. Foerster, A. Johnsen, and B. Kempenaers.** 2006. Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Animal Behaviour* 72: 531–538. <https://doi.org/10.1016/j.anbehav.2005.10.022>
- Poulin, J.F., E. D'Astous, M. Villard, S.L. Hejl, K.R. Newlon, M.E. McFadden, J.S. Young, and A. Ghalambor.** 2020. Brown Creeper (*Certhia americana*). In *Birds of the World*. Edited by A.F. Poole. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.brncr.01>
- Poulin, J.F., M.-A. Villard, M. Edman, P.J. Goulet, and A.-M. Eriksson.** 2008. Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper

- (*Certhia americana*), as conservation targets. *Biological Conservation* 141: 1129–1137. <https://doi.org/10.1016/j.biocon.2008.02.012>
- R Core Team.** 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Santema, P., M. Valcu, M. Clinchy, L. Zanette, and B. Kempenaers.** 2019. Playback of predator calls inhibits and delays dawn singing in a songbird community. *Behavioral Ecology* 30: 1283–1288. <https://doi.org/10.1093/beheco/arz075>
- Sault Ste. Marie Region Conservation Authority.** 2015. Sault Ste. Marie: Hiawatha Highlands Conservation Area. Accessed 2 November 2016. <http://ssmrca.ca/conservation-areas/hiawatha-highlands-conservation-area>.
- Staicer, C.A., D. Spector, and A. Horn.** 1996. The dawn chorus and other diel patterns in acoustic signaling. Pages 426–453 in *Ecology and Evolution of Acoustic Communication in Birds*. Edited by D.E. Kroodsma and E. Miller. Cornell University Press, Ithaca, New York, USA.
- Suter, S.M., D. Ermacora, N. Rieille, and D.R. Meyer.** 2009. A distinct reed bunting dawn song and its relation to extrapair paternity. *Animal Behaviour* 77: 473–480. <https://doi.org/10.1016/j.anbehav.2008.11.002>
- Tyler, W.M.** 1948. Brown Creeper. Pages 56–79 in *Life Histories of North American nuthatches, Wrens, Thrashers and Their Allies*. Edited by A.C. Bent. Bulletin of the United States National Museum 195. <https://doi.org/10.5479/si.03629236.195.1>
- Wickham, H.** 2016. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York, New York, USA. <https://doi.org/10.1007/978-0-387-98141-3>
- Winter, J.** 2020. A bioacoustic comparison of song structure in two populations of Brown Creeper *Certhia americana americana*. B.Sc. thesis, Algoma University, Sault Ste. Marie, Ontario, Canada.
- Wood, S.** 2018. Mixed GAM computation vehicle with automatic smoothness estimation. Accessed 24 August 2018. <https://cran.r-project.org/web/packages/mgcv/mgcv.pdf>.
- Zhang V.Y., A. Celis-Murillo, and M.P. Ward.** 2015. Conveying information with one song type: changes in dawn song performance correspond to different female breeding stages. *Bioacoustics* 25: 19–38. <https://doi.org/10.1080/09524622.2015.1076348>
- Zuur, A.F., E.N. Ieno, N. Walker, A.A. Saveliev, and G.M. Smith.** 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science and Business Media, New York, New York, USA. <https://doi.org/10.1007/978-0-387-87458-6>
- Zuur, A.F., A.A. Saveliev, and E.N. Ieno.** 2014. *A Beginner's Guide to Generalised Additive Mixed Models with R*. Highland Statistics Ltd., Newburgh, United Kingdom.

Received 13 September 2018

Accepted 14 May 2020

Associate Editor: W.D. Halliday

#### SUPPLEMENTARY MATERIAL:

**TABLE S1.** Summary of recording dates from 11 autonomous recording units deployed 2015–2017 including recorder failures and the mean ( $\pm$  SE) length of post-sunrise recording.

**TABLE S2.** Results of binomial generalized additive mixed models for the presence/absence i) of Brown Creeper (*Certhia americana*) songs ( $n = 1335$ ) and ii) pre-dawn singing ( $n = 726$ ), including the estimated degrees of freedom (edf) for the smooth term, total variance explained (adjusted  $r^2$ ), SE, and  $F$ -,  $t$ -, and  $P$ -values.

**TABLE S3.** Results of generalized additive mixed models for i) start time relative to sunrise and ii) total duration of Brown Creeper (*Certhia americana*) dawn chorus, including the estimated degrees of freedom (edf) for the smooth term, total variance explained (adjusted  $r^2$ ), SE, and  $F$ -,  $t$ -, and  $P$ -values ( $n = 466$ ).

**TABLE S4.** Results of generalized linear mixed models for Brown Creeper (*Certhia americana*) pre-sunrise song rate (songs/min;  $n = 466$ ) and comparison of pre- and post-sunrise song rate (songs/min;  $n = 808$ ).